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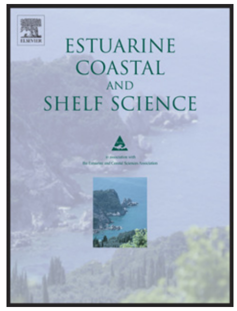

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Highlights:

- A regime-shift occurred in the Limfjord ecosystem in the mid-1990s
- The shift is parallel to those seen in adjacent seas
- Ecosystem under stress possibly trigged by extreme climate events
- Regime shift towards lower trophic level

Integrated trend assessment of ecosystem changes in the Limfjord (Denmark): evidence of a recent regime shift?

Maciej T. Tomczak[a,b,*], Grete E. Dinesen[c], Erik Hoffmann[a], Marie Maar[d] and Josianne G. Støttrup[c]

[a] Section for Marine Management, National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot, Jægersborg Allé 1, DK-2920 Charlottenlund, Denmark.

[b] Baltic Nest Institute, Stockholm University, Kräftriket 10, SE-106 91 Stockholm, Sweden.

[c] Section for Coastal Ecology, National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot, Jægersborg Allé 1, DK-2920 Charlottenlund, Denmark.

[d] Aarhus University, Department of Bioscience, Frederiksborgvej 399, PO Box 358, 4000, Roskilde, Denmark.

E-mail addresses: maciej.tomczak@stockholmresilience.su.se (M. T. Tomczak), gdi@aqua.dtu.dk (G. E. Dinesen), eh@aqua.dtu.dk (E. Hoffmann), mam@dmu.dk (M. Maar), jgs@aqua.dtu.dk (J. G. Støttrup).

*Corresponding author, Maciej T. Tomczak: E-mail addresses: maciej.tomczak@stockholmresilience.su.set tel. +46 73 460 49 12.

ABSTRACT

An integrated ecosystem assessment was carried out for the Limfjord over the period from 1984 to 2008 to describe changes in ecosystem structure and potentially important drivers. The Limfjord is an eutrophic transitional Danish fjord system with the main inflow from the North Sea in the west and main outflow to the Kattegat in the east. We showed that from 1990 to 1995, the ecosystem structure shifted from dominance by demersal fish species (eel pout,

whiting, flounder, plaice) to that of pelagic fish species (sprat, herring, sticklebacks), small-bodied fish species (black goby, pipefish), jellyfish, common shore crab, starfish and blue mussels. We interpret this change as a regime shift that showed a similar temporal pattern to regime shifts identified in adjacent seas. The observed changes in trophic interactions and food web reorganisation suggested a non-linear regime shift. The analyses further showed the regime shift to be driven by a combination of anthropogenic pressures and possible interplay with climatic disturbance.

Key words: Regime shift, Ecosystem state, Coastal waters, Structural changes, Management tool

1. Introduction

Marine ecosystems worldwide suffer from increasing anthropogenic pressures. Major changes in ecosystem structure and function have been reported from several regions, affecting the human use of resources. These changes are sometimes called regime shifts. Regime shifts, as defined by Collie et al. (2004), are ‘low-frequency, high-amplitude changes in aquatic systems that may be especially pronounced in biological variables and propagate though several trophic levels’. Moreover, some ecosystems respond with hysteresis, while others may be irreversible at the decadal scale (or more). An integrated assessment of system changes provides the background for understanding ecosystem dynamics, processes and state, and is thus important for adapting resource management accordingly (Rothschild and Shannon, 2004; Folke et al., 2004; Shannon et al., 2008).

Regime shifts have been reported from the Black Sea (Daskalov et al., 2007), the Bering Sea (Rodionov and Overland, 2005), the Benguela ecosystem (Cury and Shannon, 2004; Howard et al., 2007), the Gulf of Alaska (Heymans et al., 2007), and the Northern Pacific Ocean (Hare and Mantua, 2000). In waters adjacent to the Limfjord (Denmark), regime shifts have been detected in the North Sea in the late 1980s (Alheit et al., 2005), the Central Baltic Sea in the late 1980s (Möllmann et al., 2008), the Sound, Øresund, between Sweden and Denmark in the late 1980s and mid-1990s (Lindegren et al., 2010) and in the Danish Ringkøbing Fjord in 1997 (Petersen et al., 2008).

Hitherto, a regime shift has not been proven to have occurred in the Limfjord, neither empirically nor at the integrated assessment level, although changes in the ecosystem have been reported (Hoffmann, 2005, Christiansen et al., 2006; Krause-Jensen et al., 2011b). In the Limfjord, total nitrogen (N) and phosphorous (P) loadings have increased six-fold since the early 1900s, and peaked in the mid-1980s. The Danish Parliament decided in 1987 upon a water action plan to reduce N and P loadings in order to protect the groundwater and prevent structural changes in aquatic systems. Since then, loadings have decreased by 33% (N) and 67% (P) (Krause-Jensen et al., 2011b). Nutrients have, therefore, been and still are considered a major bottom-up forcing factor in the system. The Limfjord finfish fishery declined dramatically in the 1980s and a concurrent increase in blue mussel, *Mytilus edulis* L., biomass supported a thriving mussel fishery, which then became the largest ever economic harvest yield from the fjord (Hoffmann, 2005).

The aim of this paper is to investigate the hypothesis that a regime shift had occurred in the Limfjord since the mid-1980s. We investigated rapid changes in the Limfjord ecosystem at a decadal scale, focusing on a probable regime shift in the biotic system component using an Integrated Trend Assessment (ITA) framework.

2. Materials and methods

2.1. The study site

The Limfjord is the largest Danish fjord system with a surface area of 1.500 km^2, and a mean depth of ~6 m. It connects to the North Sea in the west and to the Kattegat in the east (Fig. 1) with a small tidal amplitude (<1 m). Due to large freshwater influxes, salinity ranges between 0-34 in some embayments. However, an overall salinity gradient decreases from west to east (from 34 to 26). The fjord system is eutrophic and suffers from frequent and extensive periods of hypoxia and anoxia during the summer months (Maar et al., 2010).

2.2. Time series data

Time series data for the ITA covered the period 1988-2008 and were selected based on their ecological importance and completeness of the time series. In total, 19 biological variables, 4 fisheries related variables and 21 abiotic variables related to environmental and climatic conditions were included in the ITA (Table 1). There were initially 85 possible abiotic variables, but due to cross-correlations we only included variables with pairwise correlation coefficients <0.8 (see Appendix Table 5). The abiotic variables were separated into 9 anthropogenic and 12 climatic pressures. Time series of the selected climatic variables started earlier in 1984 to account for a time-lag in the response of biological variables. Since the ITA needs complete time series, missing values in the data sets were replaced by averages based on the neighbouring ±2 years. For statistical analyses, data were transformed (*ln* (x+1)) to improve linearity between variables and reduce the relationship between the mean and the variance. For visualising individual time series temporal development and preliminary identification of extreme values, anomalies are displayed in the Appendix (Figures 5 to 7).

2.3. Biological variables

Data for phytoplankton Chl. *a*, polychaetes, molluscs, crustaceans and echinoderms originated from national and regional environmental monitoring programmes, and were retrieved from the common national marine database accessible online (http://MADS-en.dmu.dk). The 'Hoffmann jellyfish-index' is the percentage of trawls that could not be made due to overloading of the fishing nets by jellyfish in the Limfjord (Hoffmann, 2005; Møller and Riisgård, 2007; Riisgård et al., in press) and can be used as a proxy for jellyfish biomass. Catch per unit effort (CPUE) estimates from fish survey data were used as a proxy for fish biomass. CPUE time series data for targeted and non-commercial fish species originated from monitoring survey cruises in the Limfjord and were retrieved from the DTU Aqua (Technical University of Denmark, National Institute of Aquatic Resources) database (BABELFISH, www.aqua.dtu.dk). Time series data for herring and flounder were calibrated to adjust for a change in 1995 in type of fishing gear used to monitor fish (Dinesen, unpublished results).

2.4. Abiotic and fisheries variables

Environmental time series data (Table 1) related to nutrient levels (nutrient loadings and winter concentrations) and climate impacts (temperature, salinity, oxygen, water visibility, primary production) were retrieved from the common national marine database accessible online (http://MADS-en.dmu.dk). Phytoplankton primary production was considered as a proxy for the effect of bottom-up processes on food supply to higher trophic levels. Wind data were obtained from the Danish Metrological Institute (www.dmi.dk, Karup). Fisheries data on landings of blue mussels, decapods, pelagic and demersal fish species in the Limfjord were retrieved from account statistics of the Ministry of Food, Agriculture and Fisheries (www.fvm.dk). Fisheries yields were not treated as a biological variable because they do not necessarily reflect changes in stock biomass, but also depend on many other factors such as market price, catch quotas and other management regulations.

2.5. Integrated Trend Assessment approach and statistical methods

The ITA was developed under the umbrella of the ICES/HELCOM Working Group on Integrated Assessment of the Baltic Sea (WGIAB) (ICES, 2007, 2008, 2009, 2010; Möllmann et al., 2009; Diekmann and Möllmann, 2010). In this study, a series of statistical methods and plotting procedures were applied as described in Diekmann and Möllmann (2010) and Lindegren at al. (2010): 1) Sequential *t*-test analyses of regime shifts (STARS) on raw time series, 2) Principal Component Analyses (PCA), 3) STARS on PCA scores, 4) Chronological Clustering (CC) and 5) Traffic Light Plotting (TLP).

2.5.1. STARS on raw time series data

STARS is a discontinuity analysis, which generate Regime Shift Indices (RSI). RSI were calculated for each time series in order to detect significant shifts in mean values. The two parameters that control the scale and magnitude of potential regime shifts were set a priori. The significance level (α) was set to 0.05, and the cut-off length (l) to eight years. The latter defines the minimum length of the time period to be identified by the test. Shifts with a higher magnitude, however, can still be detected for shorter periods. The average value of the regimes was also affected by the handling of outliers. For this, Huber's weight parameter, which controls the identification and weights assigned to outliers, was set to 3. This means that if the deviation of a measurement from the expected regime average, normalized by the standard deviation for the respective section is >3, its weight is inversely proportional to the distance from the expected mean value of the new regime. Cumulative RSI based on the raw time series data (see method in Rodionov, 2004) were estimated and displayed for visual inspection of the timing of possible changes. The STARS software is available as an MS EXCEL add-in (at www.BeringClimate.noaa.gov).

2.5.2. Principal Component Analysis (PCA)

PCA was used to extract the most important modes of variability in the time series and to estimate a combined index of ecosystem states and impacts (Möllmann et al., 2009). Standardized PCAs, based on a correlation matrix, were carried out for the transformed values of time series of entire dataset (all), and for each of the subsets described above. Combined scores of PC1 for the biological variables were interpreted as an index of food-web state (biol) and those for the abiotic variables (abiol) as an index of pressure (Möllmann et al., 2008, 2009; Diekmann and Möllmann, 2010). Subset combined scores of PC1 of anthropogenic (anthropo) and climatic (clim) variables respectively, served as separate indices to improve the understanding of different pressures, and thereby improve management application. Yearly scores along the two principal components, PC1 and PC2, were plotted against time to visualize temporal relationships and the occurrence of abrupt ecosystem changes. The first factorial plane was visualised as correlation biplots, where the variable loadings, i.e. the length and orientation of the vectors, visualise the degree of correlation with the respective PC. The PCAs were performed using R (www.r-project.com).

2.5.3. STARS on PCA scores

A further STARS was carried out to detect sudden changes in the PC1 scores to identify whether abrupt changes had occurred in the overall system (ICES, 2008; Möllmann et al., 2009). Parameters for this analysis are the same as described in section 2.6. Because of the overall length of the time-series and the embedded regimes, a pre-whitening procedure to remove red-noise component from the time-series was not used (Rodionov, 2006).

2.5.4. Chronological Clustering (CC)

A second type of discontinuity analysis, CC, was carried out to identify the years in which the largest shifts in the mean value of the time-series occurred, independently of the STARS results. This method is a grouping of sequential years based on a time-variable matrix. This method describes discontinuities in a multivariate series of samples and takes into account the sequence of sampling, which makes it possible to eliminate singletons (Legendre et al., 1985;

Legendre and Legendre, 1998). To demonstrate the most important breakpoints in the dataset, the significance level (α), which can be considered as a clustering-intensity parameter, was set to 0.05 and the connectedness level to 50%. In accordance with the use of the correlation coefficient in the PCA, data were first normalized and the Euclidean distance function then calculated to determine between year similarities. The CC analyses were carried out using BRODGAR 2.5.6 (www.brodgar.com).

2.5.5. Traffic Light Plot (TLP)

TLPs were generated to visualise overall systematic patterns based on single time-series (Link et al., 2002). The raw values of each variable were categorized into quintiles and each one of these was assigned a specific colour: green for the lowest (0-20%), red for the highest (80-100%) and a gradation of colours in between. The variables were then sorted in descending order according to their PC1 loadings and plotted against years to visualize temporal patterns. The TLP was performed using R (www.r-project.com).

3. Results

In the first inspection of data from STARS applied to each raw time series data, the cumulative RSI indicated the following potential periods of regime shifts: 1991-1994, 1997-1998 and 2003-2007 (Fig. 2). Interpretation of the changes occurring in 2006-2007 was uncertain because it was towards the end of the time series.

3.1. Ecosystem changes

The results of the PCAs are shown in Figure 3. The first column of graphs presents the temporal development of PC1 and PC2 scores. A positive or negative trend in the scores indicates changes in pressures or states. The second column of graphs presents time trajectories of PC1 and PC2 scores, and the third column shows the degree of correlation of each given variable with the respective PC (see also Appendix Table 6).

PCA results for all variables are shown in Figure 3A-C. $PC1_{all}$ explained 26% and $PC2_{all}$ 13% of all variability. PCA results showed an increase in $PC1_{all}$ scores with a shift to positive values around 1995 and no clear pattern for the importance of the variables. The variables with the highest eigenvalue were for $PC1_{all}$ (Fig. 3C): landings of benthic and pelagic fish species and crustaceans, phosphorus concentrations (winter and summer) and eelpout biomass. For $PC2_{all}$ these were: salinity, oxygen and nitrogen concentrations (average annual salinity, annual average of water column oxygen and winter nitrogen concentrations), phytoplankton Chl. *a* and plaice biomass.

The biological variables (Fig. 3D-F) showed a similar temporal trend for both $PC1_{biol}$ and $PC2_{biol}$. $PC1_{biol}$ explained 21% and $PC2_{biol}$ 15% of all variability. The shift to positive values occurred between 1995 and 2000. The variables with the highest eigenvalue were for PCA_{biol} (Fig. 3F): biomass of plaice, dab and eel pout. For $PC2_{biol}$ these were: jellyfish, polychaetes, echinoderms, black goby, and pipefish. These results thus revealed the two main assemblages of organisms that exhibited the largest changes over the time period in the ecosystem.

For the abiotic variables (Fig. 3G-I), $PC1_{abiol}$ and $PC2_{abiol}$ explained 35% and 16% of the variance. The pressure index showed a negative trend with a shift to negative values in 1995 and with highest correlations to the following variables: phosphorus concentrations (summer and winter), nitrogen loadings (spring) and landings (crustaceans and benthic and pelagic fish). These results indicated the main groups of pressures which simultaneously affected the system.

PCA on climatic variables are shown in Figure 3J-L. The first two PC_{clim} explained 39% and 28% of the variability, respectively. Variables most correlated with $PC1_{clim}$ index were:

water column oxygen concentrations (summer and annual average), wind power and winter water column temperatures. Climatic related PC indices showed no clear temporal trends, however both PCs displayed abrupt extreme changes to positive values in the late 1980s, after which they fluctuated both highly and frequently around zero. These results demonstrated the main relationships between the climatic variables. They also highlighted the extreme climate fluctuations sometime observed in connection with regime shifts.

For the anthropogenic variables, the first two PCs explained 46% and 20%, respectively (Fig. 3M-O). The $PC1_{anthro}$ showed an overall decreasing trend, indicating that human pressures in the late 1990s were different to those in the 2000s. The most important anthropogenic variables in the $PC1_{anthoro}$ (Fig. 3O) were: winter phosphorus concentration, landings of crustaceans, and of pelagic and benthic fish. For $PC2_{anthro}$ these were: nitrogen loadings (winter and summer) and water visibility.

Results of STARS on PC1 showed a sudden system change in 1996 (Table 2), which is interpreted as a regime shift. The results showed that changes in climate and anthropogenic variables occurred before the changes in the biota in 1996. This suggested a system, disturbance by climate events in 1988 and 1994 superimposed on anthropogenic impacts in 1996.

Most of the shifts in the 1990s were detected by CC (Table 3). In comparison to the STARS on PC indices, changes in biota were detected only in 1991, possibly as an effect of changes in climatic drivers in 1987. At a lower significance level ($p<0.1$, not shown), however, CC on biological variables gave similar results to the STARS analyses with discontinuity in 1997 and 2001. This indicated further system changes.

3.2. Characteristics of changes

To give a more detailed visualization of the detected regimes and temporal changes, the TLPs of the biological variables and abiotic pressures from the Limfjord are shown in Figures 4A-D. For biota (Fig. 4A, Appendix), one group of variables, (plaice, dab, eelpout as well as whiting and molluscs) generally displayed a decreasing biomass trend, while another group (crustaceans, herring, three-spined stickleback, horse mackerel, pipefish, smelt, polychaetes and echinoderms) showed an increasing temporal biomass trend. Hence, there was a clear domination of demersal fish species in the period 1986-1991. After 1996, a second group of organisms more associated with pelagic food-web components and benthic opportunistic species became dominant. In the period between 1991 and 1996 there was no clear pattern and the system seemed to be in a transitional state.

Parallel to this, one group of abiotic variables (landings of crustaceans and pelagic fish, and oxygen) displayed a generally increasing temporal trend, while another group (landings of benthic fish, phosphorous and nitrogen loadings, primary production) showed a generally negative trend (Fig. 4B). For the climatic subset, it is difficult to distinguish and characterize separate periods (Fig. 4C). However, there is a short period from 1987 to 1993, where wind speeds, temperatures (winter and spring), salinities and oxygen concentrations all generally became higher than the mean values. This combination may have acted as a short-term, high frequency, system disturbance possibly triggering a regime shift in the Limfjord.

By separately considering the manageable, anthropogenic variables and the shifts detected in the mid-1990s and 2004 by STARS and CC, we can distinguish different human driving conditions (Fig. 4D). In 1996, we noticed a shift in the pressure characteristics. It changed from a system with high nutrients levels, high fishing pressures on demersal fish species and blue mussels, low fishing pressures on pelagic fish species and poor oxygen conditions, to a system characterised by increased fishing pressures on pelagic fish species, lower nutrients levels and improved oxygen conditions. The last period after 2004 could be characterized by low nutrients and higher importance of landings of pelagic fish species and crustaceans.

4. Discussion

There are several definitions of a regime-shift (Lees et al., 2006). Most of them state that regime shifts include phenomena such as changes in species abundance, community composition and trophic organisation that occur concurrently with physical changes in the climate system, resulting in an alternate stable state (McKinnell et al., 2001, Wooster and Zhang, 2004, Cury and Shannon, 2004). Collie et al. (2004) defined regime shifts as low-frequency, high amplitude, changes in oceanic conditions that may propagate through several trophic levels and that were especially pronounced in biological variables. Regime shifts may be classified according to different driver-response relationships, as linear, sudden or discontinuous (Collie et al., 2004.). Regime shifts may be caused by climatic, biogeochemical or ecological changes (Lees et al., 2006), as well as changes in management (Folke et al., 2004). Our findings satisfy the conditions of a regime-shift perception over the investigated time frame.

The present study demonstrated for the first time a regime shift in the Limfjord, which took place in the early 1990s and continued to mid-1990s. This regime shift resulted in an altered ecosystem structure dominated by lower trophic levels. The ecosystem changed from a dominance of larger demersal fish species to that of pelagic fish, small demersal fish, blue mussels, crustaceans and jellyfish. The change took a place after high amplitude occurrence in come climatic variables in the late 1980s.

4.1. Data and the Integrated Trend Assessment (ITA) approach

The approach for ecosystem assessment was developed by the ICES Working Group on Integrated Assessment of the Baltic Sea (ICES, 2007, 2008, 2009, 2010) and broadly discussed in several studies (Möllmann et al., 2008; Diekmann and Möllmann, 2010; Lindegren et al., 2010). These studies emphasised the importance of including data that represents major forcing factors and all trophic levels of a system. Data used in the present study fulfilled these criteria, except for the lack of zooplankton time series data, and the use of a proxy index for jellyfish. The lack of zooplankton data may cause a delay in the detection of a regime shift due to a fast turnover rate of the zooplankton community and response to climatic variables, such as temperature. On the other hand, the inclusion of several benthic invertebrate time series data increased the strength of our analysis relative to other regime shifts studies, such as the Baltic Sea (Möllmann et al., 2009), the North Pacific Ocean (Overland et al., 2008) and the Southern Benguela (Cury and Shannon, 2004). Inclusion of benthic invertebrate data was crucial in our study because the results showed a regime shift towards lower trophic levels in the entire ecosystem and not only of the pelagic variables and the fish community.

4.2. Changes in the Limfjord system

The persistent anthropogenic forcing variables observed in this study indicated that the regime shift included both bottom-up (nutrient loadings and climate) and top-down (fishery) forcing in accordance with previous studies (Möllmann et al., 2008, 2009; Lindegren et al., 2010).

In the Limfjord, nitrogen and phosphorous loadings have been, and still are, major bottom-up forcing factors in the system. The increase in nutrients during the last century caused a decrease in water clarity, recurrent events of anoxia and a decrease in the depth distribution of eel grass (Krause-Jensen et al., 2011a, b). Eelgrass serves as a nutrient sink and sediment stabiliser (Pedersen, 1995; Carr et al., 2010) and is generally considered to be an important juvenile fish habitat (Pihl et al., 2006). Since the 1980s, loadings have decreased by 33% (N) and 67% (P) (Krause-Jensen et al., 2011b), without any noticeable improvement in ecosystem state (Christiansen et al., 2006). The results also identified extreme high amplitude climate disturbances in temperatures, wind speeds and oxygen conditions in 1987-1989 and again in 1993-1994 that most likely triggered the regime shift in a system already under long-term anthropogenic pressure.

The top-down anthropogenic pressure was caused by commercial finfish fisheries in the beginning of the study period where after there was a constant decline of fisheries until a collapse in the mid-1990s. These fisheries were based on eel, cod, flatfish, and adult herring, and date back to the 19th century (Hoffmann, 1994, 2005). It is noted that the decline in the fisheries had started prior to the study period, and being gradually replaced by a blue mussel fishery since the 1980s (Hoffmann, 2005, 2009). In order to restore the function of the Limfjord ecosystem towards a thriving fish community, it is necessary to understand the underlying causes of the regime shift.

The shift from a dominance of equilibrium species (long lived fishes with low tolerance for bad environmental condition) to more opportunistic pelagic species (small, short lived with high tolerance for bad environmental conditions) demonstrated in this study, suggests changes in the internal structure of the ecosystem. This ecosystem reorganisation is possibly an indicator of a non-linear regime shift. This study was not able to determine whether bottom-up or top-down processes were the most important drivers of this regime shift. But as a first step, it was important to identify whether or not a regime shift had indeed occurred. Further investigations using alternative modelling techniques are, however, necessary to distinguish between different regime shift types as described by Collie et al. (2004). Nevertheless, if this was a non-linear regime shift, restoring the ecosystem to its original state would probably require larger changes in the forcing variables than the magnitude of forcing that caused the change. If the system exhibits hysteresis, it is not possible to predict the path back to the original steady state under conditions of a continued decrease in nitrogen loading (Scheffer et al., 2001; Collie et al., 2004).

4.3. Regime shifts in the Limfjord and adjacent seas

In the mid-1980s, the North Atlantic Oscillation (NAO) and the Baltic Sea Index (BSI) shifted sharply from a negative to a positive phase, giving rise to anomalous temperatures, salinities and oxygen conditions throughout the whole area (Hänninen et al., 2000; Ottersen et al., 2001; Reid et al., 2003). In the North Sea, sea surface temperature and the distribution of key zooplankton species were the main driving forces of the regime shift (Kenny et al., 2009). In the Central Baltic Sea, the main driving forcings were salinity, oxygen conditions, the BSI and cod fisheries (Möllmann et al., 2009). These climate anomalies, by means of direct and indirect biological feedbacks, most probably induced the simultaneous regime shift observed from 1987 to 1989 in the North Sea, central Baltic Sea and the Sound (Reid et al., 1998; Beaugrand et al., 2002; Wasmund and Uhlig, 2003; Kröncke et al., 1998; Möllmann et al., 2003; Durant et al., 2004; Möllmann et al., 2009; Lindegren et al., 2010). Analogously, climate anomalies possibly also induced the regime shift in the Limfjord. The regime shift observed in the nearby Ringkøbing Fjord in 1997, was on the other hand, caused by a small increase in salinity facilitated by changed sluice management and subsequent survival of annually recruiting clams, *Mya arenaria* L.(Petersen et al., 2008).

The timing of the Limfjord regime shift detected in this study, showed a similar temporal pattern to those identified in adjacent seas (Table 4). Furthermore, there seemed to be two phases of a regime shift lasting for about four to five years (Table 4). In adjacent seas, regime shifts occurred in the late 1980s and early 1990s, i.e. a few years earlier than in the Limfjord. This delay may be due to several reasons. The lack of zooplankton time series data may have caused a small delay in the detection of the regime shift as described above. Another reason could be differences in scale, system characteristics, trophic structure (i.e. low number of species of the Limfjord compared to the North Sea) or trophic control (Kenny et al., 2009, Casini et al., 2008). Finally, the delay could be due to a not fully recognised stochastic interplay of multiple drivers at the local scale.

4.4. Management perspectives

Understanding the occurrence of regime shift is important for management. This is especially important in communicating with the general public and politicians about the changes that have occurred and the predictability of restoring the ecosystem. Because regime shifts are distinguished by persistent pressures over decadal time scales, the restoration of ecosystem functioning may necessitate management over similar time scales often conflicting with local short term political ones.

If the regime shift identified in this study is non-linear (i.e. discontinuous), the ramifications for management are large because restoring the ecosystem to its original state could require a much larger change in the forcing variables than the magnitude that caused the change. It is difficult to determine which management actions are required to restore the once thriving finfish fisheries in the Limfjord, which historically provided a steady income for the local populations. The decline in larger demersal fish abundance has also negatively affected recreational fishermen (Sparrevohn et al., 2009) and their cultural traditions related to this activity. The finfish fishery was replaced by a blue mussel fishery since the late 1980s that became the largest ever economic harvest yield from the fjord, albeit with fewer participants (Hoffmann, 2005, 2009). Recently, the blue mussel fishery has declined possibly due to decreased nutrient loadings in response to implementation of the national water action plan (Dinesen et al., 2011).

The goals of the national water action plan are to reduce the N and P loadings with 50% and 80%, respectively (Kronvang et al., 1993) that are somewhat higher than the historical levels (50 to 100 years ago) (Christiansen et al., 2006). Additionally, the major basins of the

Limfjord behave differently in response to nutrient loads due to a gradient in the levels of stratification and eutrophication emphasising the need for a more differential sub-basin management (Maar et al., 2010; Krause-Jensen et al., 2011b). Potential time lags of ecosystem responses to reduced nutrient emissions may be a further complication for management, both in achieving its goals and communicating results. It would thus be appropriate for management to explore different management scenarios as described in Dinesen et al. (2011) and Hopkins et al. (2011).

The complexity of the ecosystem, multiple potential forcing variables and ecosystem resilience masking responses to human activities (and climate change) requires the functional integration of resource management and nature conservation including both socio-economic and ecological perspectives.

4.5. Concluding Remarks

We conclude that at a decadal scale a regime shift occurred recently in the Limfjord according to the definition and classification by Collie et al. (2004). We further conclude that it was possibly a non-linear regime shift. Regime shifts at a decadal scale may appear only as small fluctuations on a millennial scale. They are, however, highly important for management in terms of the use of natural resources. This study has demonstrated a shift, which occurred between early and mid1990s, changing from a biota characterised by a dominance of demersal fish to a system dominated by planktivore feeders and benthic opportunistic species.

In the Limfjord, the climatic driver is considered to be superimposed on anthropogenic drivers; including bottom-up (nutrient loadings) and top-down (fisheries) forcing that caused main changes in the ecosystem.

The timing, phasing and duration of the detected Limfjord regime shift were similar to the shifts occurring in adjacent seas, where regional climatic anomalies have been proposed as drivers. Identification of regime shifts is important for management of human activities that may cause either reversible or irreversible changes that substantially impact ecosystem goods and services.

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References

Alheit, J., Möllmann. C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., Wasmund, N., 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science 62, 1205–1215.

BABELFISH, www.aqua.dtu.dk (accessed on: 20.05.2010).

Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A. and Edwards, M., 2002. Reorganisation of North Atlantic marine copepod biodiversity and climate. Science 296, 1692–1694.

Carr, J., Odorico, P.D., McGlathery, K., Wiberg, P., 2010. Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with sediment resuspension and light attenuation. Journal Geophysical Research 115, 1-14.

Casini, M., Lövgr, J., Hjelm, J., Cardinale, M., Molinero, J.C., Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society Biological Science 275, 1793–1801.

Christiansen, T., Christensen, J.T., Markager, S.S., Petersen, J.K., Mouritsen, L.T., 2006. Limfjorden i 100 år. Klima, hydrografi, næringsstoftilførsel, bundfauna og fisk i Limfjorden fra 1897 til 2003. Faglig Rapport fra DMU 578, 1-85.

Collie, J.S., Richardson, K., Steele, J.H., 2004. Regime shifts: can ecological theory illuminate the mechanisms? Progress in Oceanography 60, 281-302.

Cury, P., Shannon, L., 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Progress in Oceanography 60, 223-243.

Daskalov, G.M., Grishin, A.N., Rodionov, S., Mihneva, V., 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Science 104 (25), 10518-10523.

Diekmann, R., Möllmann, C., (Eds.), 2010. Integrated ecosystem assessment of seven Baltic Sea areas covering the last three decades. ICES Cooperative Research Report No. 302, 1-90.

Dinesen, G.E., Timmermann, K., Roth, E., Markager, S., Ravn-Jonsen, L., Hjort, M., Holmer, M., Støttrup, J.G., 2011. Mussel production and water framework directive targets in the

Limfjord, Denmark: an integrated assessment for use in system-based management. Ecology and Society 16 (4), 26. doi: org/10.5751/ES-04259-160426.

Durant, J.M., Anker-Nilssen, T., Hjermann, D.O., Stenseth, N.C. 2004. Regime shifts in the breeding of an Atlantic puffin population. Ecology Letters 7, 388–394.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmquist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution and Systematics 35, 557-581.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47, 103-145.

Heymans, J.J., Guenette, S., Christensen, V., 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. Ecosystems 10, 499-502.

Hoffmann, E., 1994. A marine ecosystem and an economic and ethnological analyses of the consequences of utilizing its biological resources. C.M. 1994 ICES/T:36

Hoffmann, E., 2005. Fisk, fiskeri og epifauna, Limfjorden 1984-2004. DFU Rapport 147-05, 1-51.

Hoffmann, E., 2009. Fisk og fiskeri i Limfjorden. Årlig rapport til Limfjordskomiteen, pp. 1-18.

Hopkins, T.S., Bailly, D., Støttrup, J.G., 2011. A systems approach framework for coastal zones. Ecology and Society 16 (4), 25.

Howard, J.A.E., Jarre, A., Clark, A.E., Moloney, C.L., 2007. Application of the sequential t-test algorithm for analyzing regime shifts to the southern Benguela ecosystem. African Journal of Marine Science 29(3), 437-451.

Hänninen, J., Vuorinen, I., Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnology and Oceanography 45, 703–710.

ICES, 2007. Report of the ICES/HELCOM Working Group on Integrated Assessment of the Baltic Sea (WGIAB), 12-16 March 2007, Hamburg, Germany. ICES CM 2007/BCC:04. 71 pp.

ICES, 2008. Report of the ICES/HELCOM Working Group on Integrated Assessment of the Baltic Sea (WGIAB), 25–29 March 2008, Öregrund, Sweden. CM 2008/BCC:04. 145 pp.

ICES, 2009. Report of the ICES/HELCOM Working Group on Integrated Assessment of the Baltic Sea (WGIAB), 16–20 March 2009, Rostock, Germany. ICES CM 2009/BCC:02. 81 pp.

ICES, 2010. Report of the ICES/HELCOM Working Group on Integrated Assessment of the Baltic Sea (WGIAB), 19–23 April 2010, ICES Headquarters, Copenhagen, Denmark. ICES CM 2010/SSGRSP:02. 94 pp.

Kenny, A.J., Skjoldal, H.R., Engelhard, G.H., Kershaw, P.J., Reid, J.B., 2009.An integrated approach for assessing the relative significance of human pressures and environmental forcing on the status of large marine ecosystems. Progress in Oceanography 81, 132-148.

Krause-Jensen, D., Carstensen, J., Nielsen, S.L., Dalsgaard, T., Christensen, P.B., Fossing, H., Rasmussen, M.B., 2011a. Sea bottom characteristics affect depth limits of eelgrass *Zostera marina.* Marine Ecology Progress Series 425, 91-102.

Krause-Jensen, D., Markager, S., Dalsgaard, T., 2011b. Benthic and pelagic primary production in different nutrient regimes. Estuaries and Coasts 35, 527-545.

Kronvang, B., Ærtebjerg, G., Grant, R., Kristensen, P., Hovmand, M. and Kirkegaard, J., 1993. Nationwide monitoring of nutrients and their ecological effects: State of the Danish aquatic environment. Ambio 22, 176–187.

Kröncke, I., Dippner, J.W., Heyen, H., Zeiss, B. 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Marine Ecology Progress Series 167, 25–36.

Lees, K., Pitois, S., Scott, C., Frid, C., and Mackinson, S., 2006. Characterizing regime shifts in the marine environment. Fish and Fisheries 7, 104–127.

Legendre, P., Legendre, L., 1998. Numerical Ecology (2nd English end). Amsterdam, The Netherlands,: Elsevier, 853 pp.

Legendre, P., Dallot, S., Legendre, L., 1985. Succession of species within a community: Chronological clustering, with applications to marine and freshwater zooplankton. American Naturalist 125, 257–288.

Lindegren, M., Diekmann, R., Möllmann, C., 2010. Regime shifts, resilience and recovery of a local cod stock. Marine Ecology Progress Series 402, 239–253.

Link, J.S., Brodziak, J.K.T., Edwards, S.F., Overholtz, W.J., Mountain, D., Jossi, J.W., Smith, T.D., Fogarty, M.J., 2002. Marine ecosystem assessment in a fisheries management context. Canadian Journal of Fisheries and Aquatic Science 59, 1429–1440.

Maar, M., Timmermann, K., Petersen, J.K., Gustafsson, K.E., and Storm, L.M., 2010. A model study of the regulation of blue mussels by nutrient loadings and water column stability in a shallow estuary, the Limfjorden. Journal of Sea Research 64, 322-333.

MADS, the national database for marine data, Department of Bioscience, Aarhus University. http://MADS-en.dmu.dk (access: 20.05.2010)

McKinnell, S.M., Brodeur, R.D., Hanawa, K., Hollowed, A.B., Polovina, J.J., Zhang, C.I., 2001. An introduction to the beyond El Nino conference: climate variability and marine ecosystem impact from the tropics to the Arctic. Progress in Oceanography 49, 1–6.

Møller, L.F., Riisgård, H.U., 2007. Population dynamics, growth and predation impact of the common jellyfish, *Aurelia aurita*, and selected hydromedusae in Limfjorden (Denmark). Marine Ecology Progress Series 346, 145–165.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., and Hinrichsen, H-H., 2003. The marine copepod *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fisheries Oceanography 12, 360-368.

Möllmann, C., Müller-Karulis, B., Kornilovs, G. and St. John, M. A., 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES Journal of Marine Sciences 65, 302-310.

Möllmann, C. Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., Axe, P., 2009. Reorganization of large marine ecosystem due to atmospheric and anthropogenic pressures: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology 15, 1377-1393.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., Stenseth, N.C., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128, 1–14.

Overland, J., Rodionov, S., Minobe, S., Bond, N., 2008. North Pacific regime shifts: definitions, issues and recent transitions. Progress in Oceanography 77, 92-102.

Pedersen, M.F., 1995. Nitrogen limitation of photosynthesis and growth: comparison across aquatic plant communities in a Danish estuary (Roskilde Fjord). Ophelia 41(1), 261-272.

Petersen, J.K., Hansen, J.W., Laursen, M.B., Clausen, P., Carstensen, J., Conley, D.J., 2008. Regime shift in a coastal marine ecosystem. Ecological Application 18(2), 457-510.

Pihl, L., Baden, S., Kautsky, N., Rönnbäck, P., Söderqvist, T., Troell, M., Wennhage, H., 2006. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuarine Coastal and Shelf Science 67, 123-132.

Reid, P.C., Edwards, M., Hunt, H.G., Warner, A.J. 1998. Phytoplankton change in the North Atlantic. Nature 391, 546.

Reid, P.C., Edwards, M., Beaugrand, G., Skogen, M., Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fisheries Oceanography 12, 260–269.

Riisgård, H.U., Andersen, P., Hoffmann, E., 2012 (in press). From Fish to Jellyfish in the Eutrophicated Limfjorden (Denmark). Estuaries and Coasts, doi: 10.1007/s12237-012-9480-4.

Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31, 1-4. L09204, doi: 10.1029/2004GL019448.

Rodionov, S.N., 2006. Use of pre-whitening in climate-regime shift detection. Geophysical Research Letters 33, 1-4. L12707, doi: 10.1029/2006GL025904.

Rodionov, S.N., Overland, J.E., 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. ICES Journal of Marine Science 62, 328-332.

Rothschild, B.J., Shannon, L.J., 2004. Regime shifts and fishery management. Progress in Oceanography 60, 397-402.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591-596.

Shannon, L.J., Neira, S., and Taylor, M., 2008. Comparing internal and external drivers in the southern Benguela and the southern and northern Humboldt upwelling ecosystems. African Journal of Marine Science 30, 63–84.

Sparrevohn, C.R., Nicolajsen, H., Kristensen, L., Støttrup, J.G., 2009. Registrering af fangster i de danske kystområder med standardredskaber fra 2005-2007. Nøglefiskerrapporten 2005-2007. DTU Aqua-rapport nr. 205-2009, 72 pp. Charlottenlund. Institut for Akvatiske Ressourcer, Danmarks Tekniske Universitet. In Danish with an English summary.

Wasmund, N., Uhlig, S., 2003. Phytoplankton trends in the Baltic Sea. ICES Journal of Marine Science 60, 177–186.

Wooster, W.S., Zhang, C.I., 2004. Regime shifts of the North Pacific early indications of the 1976–1977 event. Progress in Oceanography 60, 183–200.

Figure legends

Figure 1. The study area, the Limfjord is located in northern Denmark (inserted map). Fish and fisheries data originated from fish survey transects and account statistics of landings from the central broads. Environmental data originated from a national environmental monitoring station located in Løgstør broad.

Figure 2. Cumulative Regime Shift Indices (RSI) from STARS on the raw time series data, including all variables. RSI on the Y axis is unit-less.

Figure 3. Results of Principal Component Analyses. The first column shows the temporal trend PC1 and PC2 axis scores, the second column shows the time trajectory of PC1 and PC2 scores combines, and column three shows the dependencies between variable (for detailed values see Appendix, Table 6). Rows, from top to bottom, show the results of analyses of data sets including: all variables, biological, abiotic, climatic and anthropogenic, respectively. Please note that the scale differs between axes.

Figure 4. Traffic light plots representing the development of the Limfjord system. The time-series were transformed into quintiles and sorted according to the PC1 axis scores: (a) biota; (b) abiotic variables; (c) climatic impact; and (d) anthropogenic pressure. Solid lines represent regime shifts detected by Chronological Clustering, whereas dashed lines show the main shifts detected from the PC1 index. For abbreviations of variables, see Table 1.

Tables

Table 1. Data variables used in this study, including abbreviations, units and the period of the time series.

Table 2. Significant shifts in the PC 1 scores detected by STARS with RSI.

Table 3. Shifts in multivariate data sets detected using Chronological Clustering.

Table 4. The timing of the Limfjord regime shift compared with regime shifts detected in adjacent seas: CBS) the Central Baltic Sea; GoR) Gulf of Riga; GoF) Gulf of Finland; BoS) Bothnian Sea and BoB) Bay of Bothnia.

Appendix

Figure 5. Anomalies from the mean of biological time series subset. Note the different scales.

Figure 6. Anomalies from the mean of abiotic time series. Note the different scales.

Figure 7. Anomalies from the mean of climatic time series (begins in 1984). Note the different scales.

Table 5. Cross-correlations between used variables

Table 6. PC loadings.

Variable name	Code	Unit	Time series period
Biological			
Hoffmann Jellyfish index	JEL	%	1984-2007
Polychaetes	POL	g/m2	1984, 1986-2005
Molluscans	MOL	g/m2	1984, 1986-2005
Crustaceans	CRU	g/m2	1987-2005
Echinoderms	ECH	g/m2	1984, 1986-2005
Phytoplankton chlorophyll a, spring	Chla_spr	g 7l	1984-2007
Phytoplankton chlorophyll a, summer	Chla_sum	g/l	1984-2007
Sprat (*Sprattus sprattus*)	SPR	t/ 0.5h	1988-2008
Horse mackerel (*Trachurus trachurus*)	HMK	t/ 0.5h	1988-2008
Whiting (*Merlangius merlangus*)	WHI	t/ 0.5h	1988-2008
Dab (*Limanda limanda*)	DAB	t/ 0.5h	1988-2008
Eel pout (*Zoarces viviparus)*	ELP	t/ 0.5h	1988-2008
Plaice (*Pleuronectes platessa)*	PLA	t/ 0.5h	1988-2008
Herring (*Clupea harengus*)	HER	t/ 0.5h	1988-2008
Flounder (*Platichthys flesus*)	FLO	t/ 0.5h	1988-2008
Smelt (*Osmerus eperlanus*)	SML	t/ 0.5h	1988-2008
Black goby (*Gobius niger*)	BGO	t/ 0.5h	1988-2008
Pipefish (*Syngnathus typhle*)	PIP	t/ 0.5h	1988-2008
Sticklebacks (*Gasterosteus aculeatus aculeatus*)	STI	t/ 0.5h	1988-2008
Anthropogenic (fisheries)			
Mussel yield, landings	Y_mus	ton	1988-2012
Decapods yield, landings	Y_cru	ton	1988-2013
Benthic fish yield, landings	Y_ben	ton	1988-2014
Pelagic fish yield, landings	Y_pel	ton	1988-2015
Anthropogenic (abiotic)			
Dissolved inorganic nitrogen, summer	DIN_sum	$\mu g\ l^{-1}$	1988-2007
Dissolved inorganic nitrogen, winter	DIN_win	$\mu g\ l^{-1}$	1988-2008
Dissolved inorganic phosphor, summer	DIP_sum	$\mu g\ l^{-1}$	1988-2009
Dissolved inorganic phosphor, winter	DIN_win	$\mu g\ l^{-1}$	1988-2010
Nitrogen loadings, spring	N_lo_spr	$\mu g\ l^{-1}$	1988-2011
Nitrogen loadings, summer	N_lo_sum	$\mu g\ l^{-1}$	1988-2012
Nitrogen loadings, winter	N_lo_win	$\mu g\ l^{-1}$	1988-2013
Phosphor loadings, spring	P_lo_spr	$\mu g\ l^{-1}$	1988-2014
Nitrogen total, winter	Ntot_win	$\mu g\ l^{-1}$	1984-2007
Climate (abiotic)			
Bottom oxygen, annual average	O_2b_ann	$mg\ l^{-1}$	1984-2007
Bottom oxygen, summer	O_2b_sum	$mg\ l^{-1}$	1984-2007
Water column oxygen, annual average	O_2wc_ann	$mg\ l^{-1}$	1984-2007
Water column oxygen, summer	O_2wc_sum	$mg\ l^{-1}$	1984-2007
Phytoplankton primary production, spring	PP_spr	$mgC/m^2/day$	1984-2003
Phytoplankton primary production, summer	PP_sum	$mgC/m^2/day$	1984-2003
Salinity, annual average	Sal_ann	unit-less	1984-2007
Visibility, annual	Vis_ann	m	1984-2007
Sea surface temperature, summer	T_sum	°C	1984-2007
Sea surface temperature, winter	T_win	°C	1984-2007
Sea surface temperature, spring	T_spr	°C	1984-2007
Wind, annual	Wind_ann	m/s	1984-2007

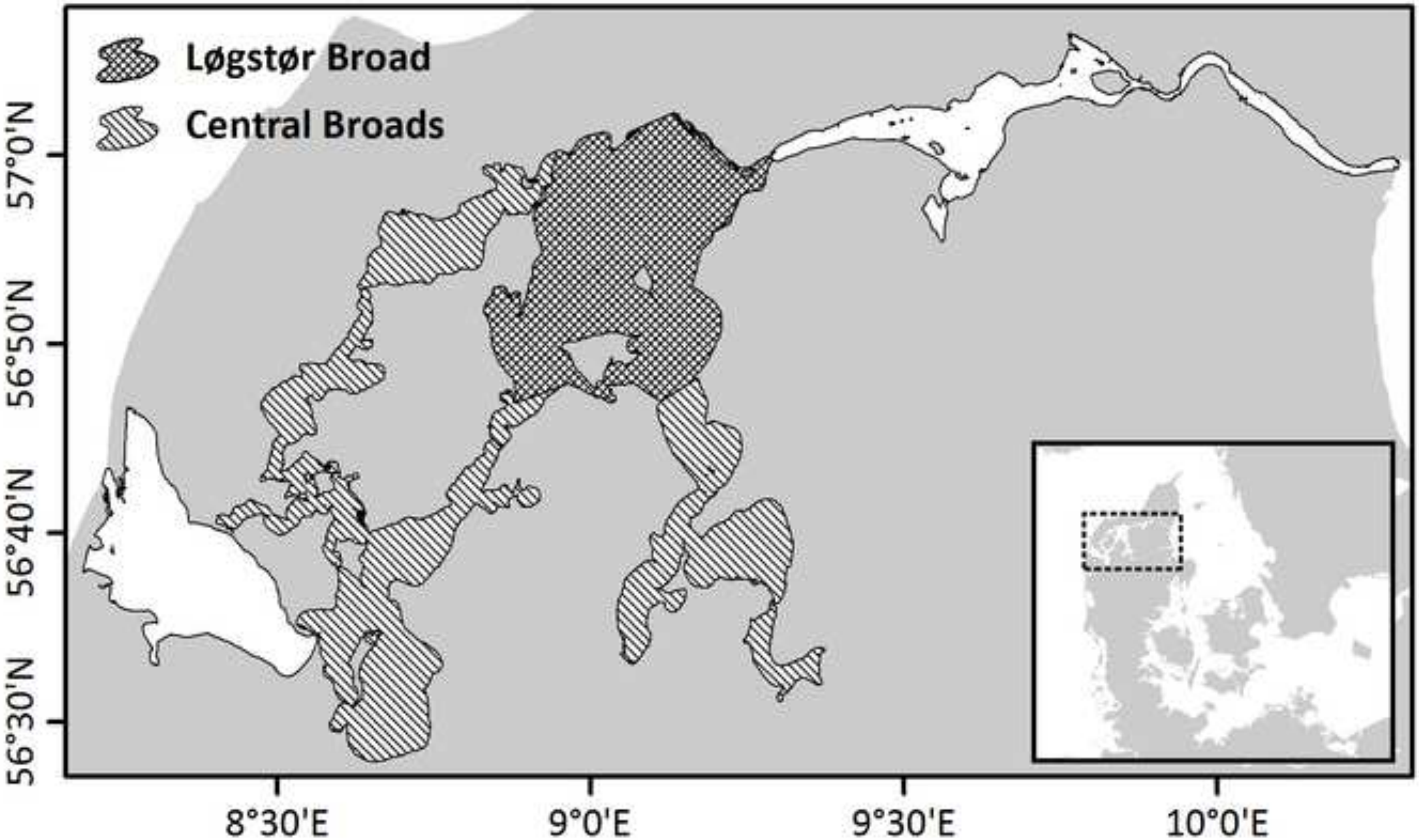
Data sets	PC1	RSI
all variables	1996	1.45
Biotic	1996	0.49
Abiotic	1996	-1.15
Anthropogenic	1996	-0.77
	2004	-0.79
Climatic	1994	0.28
	2007	-1.24
Climatic (1984-2007)	1988	0.76

Chronological cluster	shift time
Euclidian dist.	p<0.05
all variables	1991
	1995
	2005
Biotic	1991
Abiotic	1996
Anthropogenic	1993
Climatic	1993
Climatic*	1987
	1993

* time series range 1984-2007.

System	North Sea***	Limfjord	Kattegat**	The Sund*	CBS*	GoR*	GoF*	BoS*	BoB*	Kvädöfjärden*
Period studied	1983-2003	**1988-2008**	1982-2008	1979-2005	1975-2008	1973-2008	1979-2007	1983-2008	1979-2006	1971-2008
Shift 1					1984/85			1982/83		
Shift 2	1989/90	**1990/91**	1988/89	1987/88	1987/88	1988/89	1988/89	1988/89	1987/88	1988/89
Shift 3	1993/94	**1995/96**		1994/95		1997/98	1995/96		1993/94	1997/98
Shift 4				2000/2001			2002/03			2002/2003

* ICES 2010 ** ICES 2008 *** Kenny et al., 2009


Løgstør Broad
Central Broads
57°0'N
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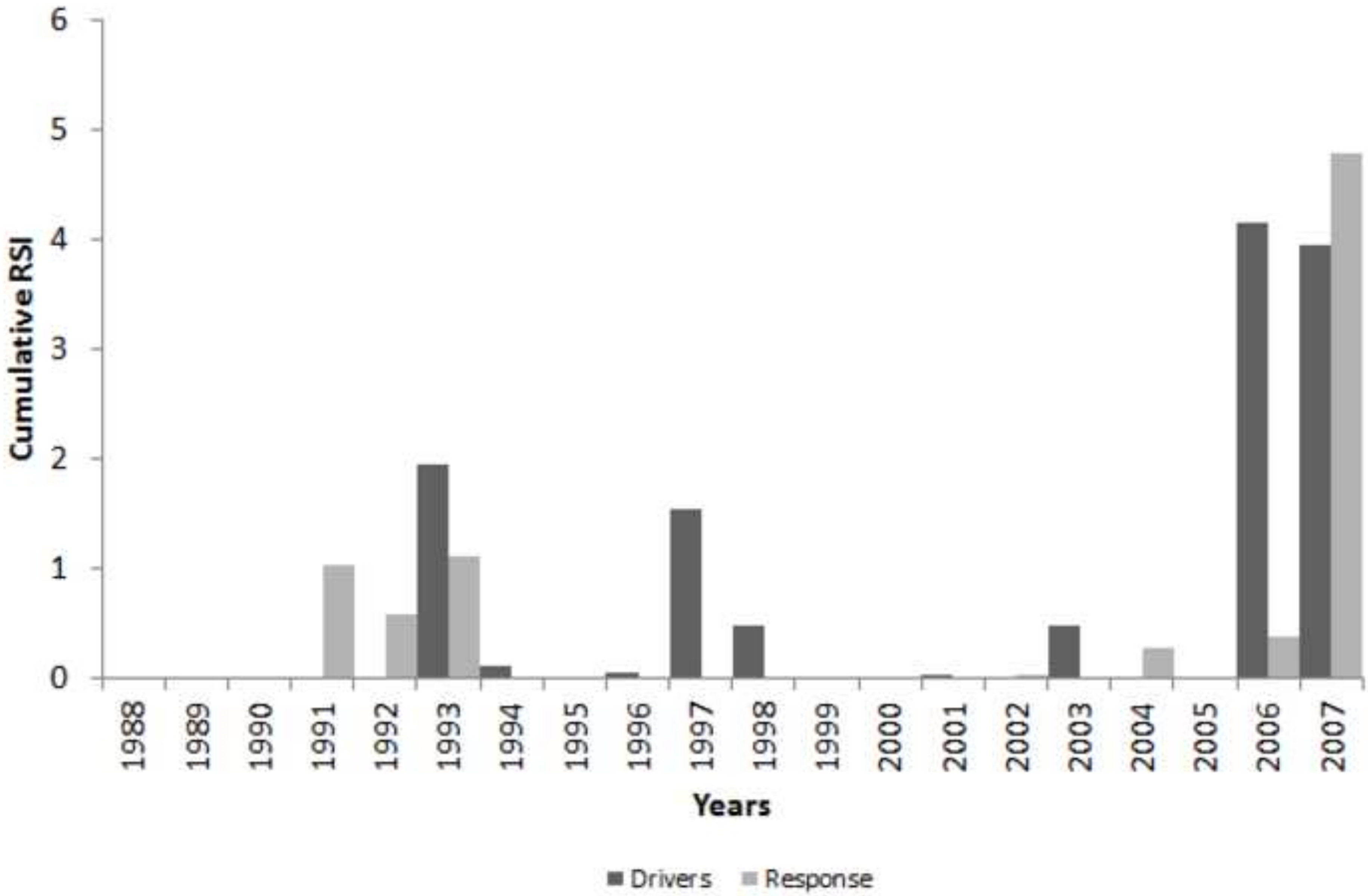
9°30'E
10°0'E

Figure(s)


Cumulative RSI
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6
1988
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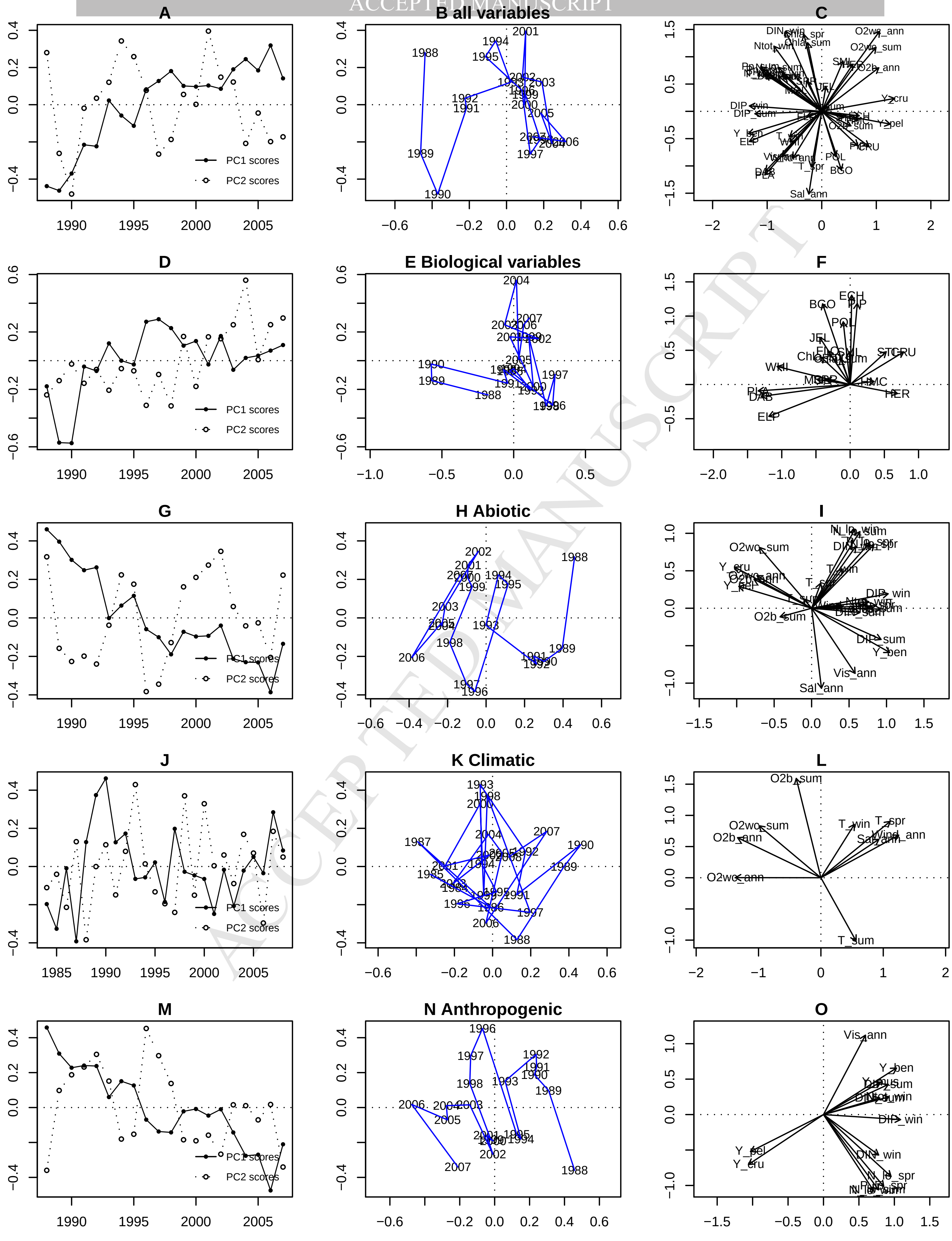
A
B all variables
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E Biological variables
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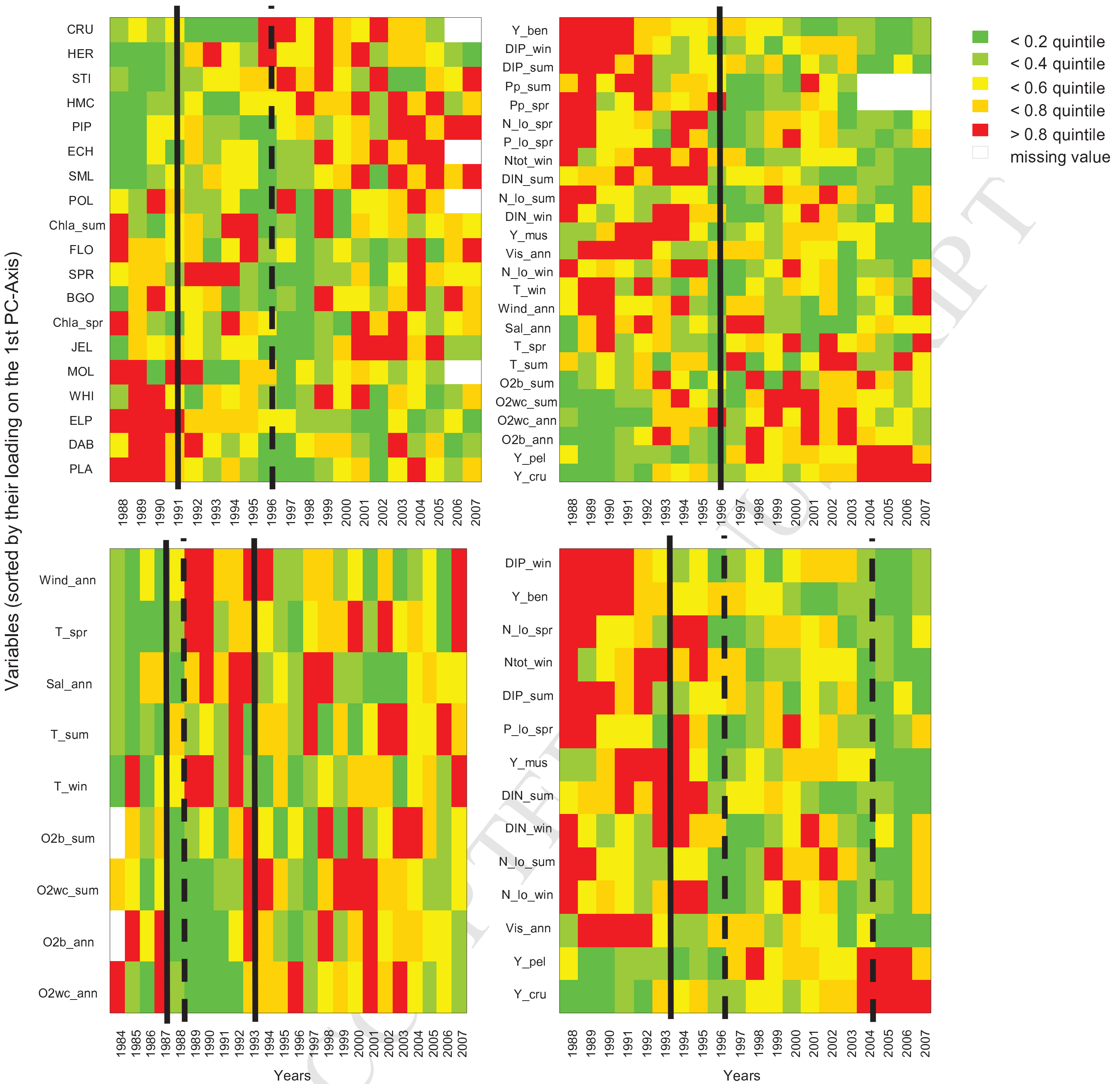
PC1 scores
PC2 scores

Figure(s)



CRU
HER
STI
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ECH
SML
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Chla_sum
FLO
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BGO
Chla_spr
JEL
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WHI
ELP
DAB
PLA
Y_ben
DIP_win
DIP_sum
Pp_sum
Pp_spr
N_lo_spr
P_lo_spr
Ntot_win
DIN_sum
N_lo_sum
DIN_win
Y_mus
Vis_ann
N_lo_win
T_win
Wind_ann
Sal_ann
T_spr
T_sum
O2b_sum
O2wc_sum
O2wc_ann
O2b_ann
Y_pel
Y_cru
< 0.2 quintile
< 0.4 quintile
< 0.6 quintile
< 0.8 quintile
> 0.8 quintile
missing value
Variables (sorted by their loading on the 1st PC-Axis)
Wind_ann
T_spr
Sal_ann
T_sum
T_win
O2b_sum
O2wc_sum
O2b_ann
O2wc_ann
Years
Years